

***Melipona yucatanica* New Species (Hymenoptera: Apidae:
Meliponinae); Stingless Bee Dispersal Across the Caribbean Arc and
Post-Eocene Vicariance**

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Abstract.—The second insular continental species of *Melipona* north of Panama is described. Its similarity to workers of the *M. favosa* group and the single meliponine species restricted to Caribbean islands, *M. variegatipes* of the Lesser Antilles, is analyzed in conjunction with the male genital capsules described here. The South American species *favosa* differs slightly but very clearly from *variegatipes*: *yucatanica* differs greatly from both, and also from all *Melipona* of Central America. Such features in the *favosa* group, and current distributions of *Melipona* in Central America, suggest that *Melipona* occupied South America and Yucatán before the late Pliocene connection via Panama. The Panamanian land bridge was crossed by other *Melipona* found both in Colombia and Costa Rica, but an ecological barrier between Costa Rica and Panama has prevented movement by competing species pairs that we suggest share common ancestors—*M. favosa*—*M. yucatanica* and *M. beecheii*—*M. compressipes*. We propose that ancestral meliponines of these and other taxa dispersed across the Caribbean arc and cannot colonize territories of their sister species. After bee dispersal, tectonic activity in the Caribbean separated populations and led to insular species in Central America and the Caribbean. Miocene fossils of Trigonini from the Greater Antilles and southern Mexico, and the broken distribution of *Ptilotrigona*, also suggest dispersal across the proto-Antillean archipelago prior to the Panama land bridge.

The colonial bee described here, *Melipona yucatanica*, is known by the Mayan inhabitants of the Yucatan peninsula as “Ts’ets” (González 1983). It is one of the smaller bees of the genus, about 8 mm in length, and its colonies are very small (<200 workers). Here we propose this bee is a member of the *M. favosa* group and demonstrate that bees from the Lesser Antilles and thought to be a geographic race of *M. favosa* are an insular species. We review biogeography of neotropical meliponines and show why current species ranges, the distribution of Miocene fossils, and parapatry in sister species of *Melipona* each suggest dispersal across a proto-Antillean archipelago between South America and Mexico before the Panama landbridge existed.

Schwarz (1932) characterized *M. favosa* as distinguishable from congeners by the relatively large inter-orbital distance, notably greater than the length of the eye. He

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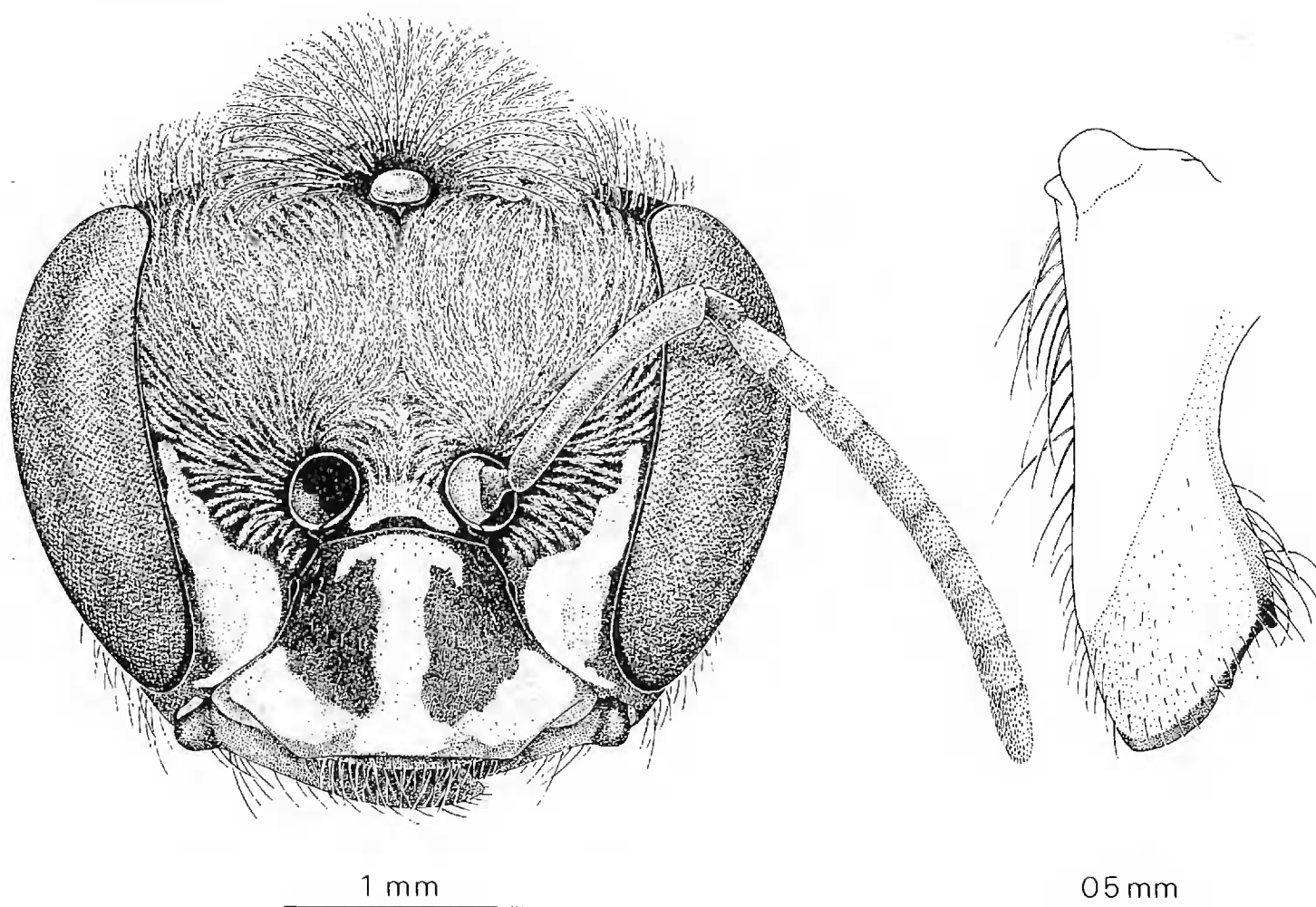
indicated a wide distribution of *M. favosa*, from Argentina to Panama. No related species was known from Central America or Mexico. Typical *Melipona favosa* (Fabricius) was described from French Guiana and occurs in the Guianas, Venezuela, Colombia and Trinidad; *M.f. orbignyi* (Guérin) was described from Chiquitos, Bolivia and occurs also in Paraguay and Brazil (Mato Grosso, Maranhão and Ceará); *M.f. phenax* Cockerell is known from Ecuador and Panama; *M.f. baeri* Vachal exists from Tucumán, Argentina to northern Bolivia, *M.f. lunulata* Friese is known from Yungas, Bolivia (Espia Rio Bopi and Canamina), and *M.f. peruviana* was described from Huancabamba, Perú. The systematic treatment of *M. favosa* by Schwarz may be in need of some modification. The northeastern Brazilian *Melipona subnitida* Ducke should be included, since it too has an unusually wide superior interorbital area. Three of the subspecies mentioned above, *orbignyi*, *baeri* and *lunulata*, probably are sympatric in Bolivia. If more intensive collecting in Bolivia reveals no hybrids, then these bees, like many geographic races recognized by Schwarz, are likely distinct species. Although the distribution of *M.f. phenax* appears anomalous, this may be due to lack of collection between Ecuador and Panama.

An insular species, *M. variegatipes* Gribodo, is known only from Guadeloupe, Dominica and Montserrat, of the Lesser Antilles. It is one of the two native species of *Melipona* in the Caribbean, and it appears closely related to *M. favosa* (Schwarz 1932; Moure 1960). Schwarz (1932) synonymized *variegatipes* with *favosa* and made it a subspecies of this taxon. We examined the male and genital capsule of *variegatipes* from Montserrat and find differences from *favosa* of Colombia (Figs. 10–23, and Discussion). The other Caribbean *Melipona* is *M. beecheii fulvipes* (sensu Schwarz 1932), which is slightly smaller than *M. beecheii beecheii* and is found in Belize, Yucatán, Jamaica and Cuba. Michener (1982) suggests that *M. beecheii fulvipes* has been brought to the islands from the mainland by indigenous inhabitants of the Caribbean, which seems to us reasonable in light of its mainland distribution and the extensive beekeeping with this species practiced by the Maya.

Description of Melipona yucatanica sp.n. Melipona fulvipes; Wille, 1976, *Rev. Biol. Trop.*, 24(1):134–135, *nec.* Guérin, 1835 *Melipona* sp. Mayan name “Ts’ets”, González 1983:193.

Worker (Figs. 1, 2); total length approximately 7.9 mm, wing length from apex to costal sclerite 6.04 mm; maximum head width 3.36 mm; maximum abdominal width 3.05 mm.

Integumental coloration.—For the most part dark brown to almost black. Mid and hind femora and tibiae light ferruginous or reddish with black markings on lower face of femora, variegately on mid tibiae, and lower third of posterior tibiae. Tarsi dark, having small light brown-ochraceous spots on posterior basitarsus; mid basitarsus bicolorous. Sterna dark. Mandible largely yellow, slightly brown and darkened in apical fifth, and having a black spot near the internal basal articulation (Fig. 2). Labrum bright yellow. Face displaying large yellow maculation in the form of an inverted ‘T’ on clypeus; supraclypeal maculation crescentic; paraocular maculations large, widest at tentorial foveae and narrowing along orbit, terminating slightly above the level of the superior alveolus. Antennae brownish, basal flagellomere slightly yellow. Scutellum and axillae yellow. Mesoscutum displaying fine yellow striation laterally, beginning at the level of the mid tegula and broadened backwards. Tergites 1 to 5 displaying yellow marginal bands, bordered by fine translucent areas



Figures 1–2. *Melipona yucatanica*, holotype worker from Mérida, Yucatán, México; head and mandible.

but lacking typical lateral spots of *favosa* (*seuso stricto*); width of bands approximately equal to diameter of mid ocellus. Tegulae ferruginous-light yellow; wing staining the same color, slightly more pronounced in the marginal and radial cell.

Vestiture.—Densely plumose, branched hairs on the head, terminating at facial maculations below the alveoli, becoming almost glabrous on paraocular areas below tentorial foveae and extremely short and sparse on most of the clypeus, and interspersed on genae with longer hairs on the basal fifth. Hairs on labrum shorter than more yellow hairs on mandibles. Hairs yellowish on mesoscutum, scutellum, pronotal lobes and basal area of propodeum; branched on mesepisternum, ventral portion of thorax, femora, pro- and mesothoracic tibiae and basal two-thirds of the anterior and all of the posterior margin of the metatibiae; light yellow-ferruginous on tarsi and anterior margins of pro- and mesothoracic tibiae and distal anterior third of metathoracic tibiae. Yellow on the metathoracic tergites, sparse in the basal two and progressively longer and denser on following segments, black hairs also appearing on last tergite.

Punctuation.—Face dull due to a very dense micropunctuation; intercalating, sparse piligerous punctures on clypeus, slightly sparser on genae, primarily found within lower one-third; the same large punctures near orbit; microreticulation replacing punctuation toward the hypostoma. Mesoscutum having sparse piligerous punctures (5 to 6 per ocellar diameter), separated by slightly more than their width;

micro-punctation dull, except small area on disc where punctures are more separated and the integument is slightly shiny. Mesepisternal piligerous punctures slightly larger than those of mesoscutum. Scutellar punctures wide, twice as large as those of mesoscutum, separated by 2 to 3 diameters, smooth and shiny; basal area of propodeum having similar punctures, some wider than those of scutellum but not separated, slightly shining, and progressively dull microtessellated toward sides. Tergites displaying micropunctation similar to that of clypeus, although smooth at the base of the second tergite, piligerous punctures less distinct. Legs having superficial microreticulation, slightly more shining and punctures more evident.

Form and proportions.—(measurements given in mm) Head broader than long (3.36: 2.68); eyes longer than twice width (2.04: 0.88), slightly shorter than superior interorbital distance and strongly convergent below (2.13: 2.24: 1.78). Clypeus shorter than two-thirds its width and this slightly larger than clypeo-ocellar distance (0.98: 1.48: 1.40). Inter-alveolar distance subequal to diameter of alveolus and smaller than alveorbital, the lateral alveocellar distance a little more than twice this (0.30: 0.32: 0.50: 1.10). Lateral interocellar distance over twice diameter of median ocellus, ocellorbital distance smaller (0.66: 0.26: 0.52). Malar space equal to half the distance from the inferior lower edge of the clypeus to the orbit and barely two-fifths diameter of the median ocellus (0.10: 0.20: 0.26). Length of scape little more than six times its diameter and greater than the lateral alveo-ocellar distance (1.16: 0.18: 1.10); length of first three flagellomeres 0.20, 0.24, 0.24, diameter of the third 0.18. Mandibles having narrow incision on apical border, approximately at three-fifths from external apex, followed by a tiny denticle greatly separated from the inner edge by a simple emargination. Forewings having marginal cell five times longer than wide, narrowly open at apex; first submarginal cell well defined; veins M and M1 extending almost to wing margin, first m-cu almost complete. Mesotibia longer than its basitarsus (2.00: 1.20); metatibia 2.5 × longer than greatest width (2.56: 1.02), terminating in a sharp angle but not forming tooth; anterior penicillus weak; metabasitarsus twice as long as wide (1.32: 0.68), having slightly convex posterior border, ending in a prominent downward-projecting angle.

Male.—(Figs. 3–9). Total length approximately 8.13 mm; fore wing length from apex to costal sclerite 6.32 mm; maximum head with 3.08 mm; maximum abdominal width 3.36 mm.

Integumental coloration.—Present material callow and incompletely pigmented; yellow maculation scarcely evident, particularly on clypeus and paraocular area. Axillae and margins of mesoscutum clearly lacking yellow markings. Metasomal bands and predominant dark body color similar to that of worker.

Vestiture.—Density and color patterns like that of workers except at the superior margins of the clypeus and inferior paraocular areas, where the dense, plumose gray pubescence is well developed.

Punctation.—Similar to that of worker.

Form and proportions.—Head wider than long (3.08: 2.44); eyes slightly longer than twice their width (1.90: 0.92), subequal to superior interorbital distance and very convergent below (1.92: 1.80: 1.36). Clypeus slightly shorter than three-fourths its width and this slightly greater than distance between the clypeus and median ocellus (0.96: 1.32: 1.12). Inter-alveolar distance little less than diameter of antennal alveolus and near five-sevenths that of the alveorbital distance; lateral alveocellar distance 2.6 times longer than this (0.24: 0.32: 0.34: 0.88). Distance between lateral

ocelli more than twice diameter of median ocellus and little less than the ocelloorbital distance (0.60: 0.24: 0.46). Malar space very short, one-fourth diameter of median ocellus (0.06: 0.24). Length of scape 3.8 times greatest diameter and slightly less than lateral alveocellar distance (0.84: 0.22: 0.88); length of first three flagellomeres 0.08, 0.32, 0.32 and diameter of third 0.18. Mandibles edentate. Wings similar to those of workers, fore wing $2.8 \times$ longer than width (6.32: 2.28). Metatibia $3.4 \times$ longer than wide (2.04: 0.60) with the apex evenly rounded and narrowed posterior and anteriorly. Metabasitarsi $2.5 \times$ longer than wide (1.20: 0.48). Eighth sternite very elongate and narrow (1.20: 0.32); hooks of valve almost straight and shorter than gonostylus (1.00: 1.40). Further details and comparison with *M. f. favosa* are given in Figs. 3–9 and 10–16.

Variation.—In several specimens the clypeus presents a yellow marking along the median line and one on each inferior edge, not completing the inverted “T” of the holotype worker. In some workers the band of the first metasomal tergite is slightly interrupted medially. Metric variation is indicated in Table 1.

Types and type locality.—Holotype worker and two paratypes of the same caste with labels “Mérida, Yucatán, México, 16.XII.80, J. G. Acereto leg.,” 26 additional paratypes from the same collector and locality, II. 1987 and 4 with the labels “Mérida, Yucatán, México, XII. 1981, Camargo leg.,” the holotype and paratypes labelled “Mérida” were taken from a nest carried to Mérida from Baxac, 20 km southwest of Tzucacab, Yucatán (Michener and J. González Acereto, personal communication), 8 paratype workers, the allotype and an additional male also taken from a nest from Yucatán collected by J. González A. bearing the labels “Mexico, Quintana Roo, F. Carrillo Puerto, 10 km N, 10 Oct. 86, D. Roubik coll.; nest from Yucatán, J. González.” Additional paratype workers (4) housed in the Snow Entomological Museum, University of Kansas, from the University of Kansas Mexico expedition; Guerrero State, 42 km N. Acapulco, and Oaxaca State, 49 km W Tehuantepec; and from Costa Rica, Puntarenas Province, 7 mi. S. Platanares. Holotype bearing red label and paratypes with yellow labels deposited in the collection of the Department of Biology of the Faculty of Philosophy, Science and Letters at the University of São Paulo in Ribeirão Preto. Allotype bearing red label and paratypes deposited with the Instituto de Biología, Universidad Nacional Autónoma de México (UNAM) in Mexico city. Paratypes also deposited at the Smithsonian Institution, Washington, D.C.; the Smithsonian Tropical Research Institute, Balboa, Panama, the collection of the Department of Zoology of the Federal University of Paraná, and the Snow Entomological Museum at the University of Kansas, Lawrence.

Distribution and bionomic notes.—According to González (1983:193) this bee is found in the southern portion of the Yucatán peninsula, in forest remaining in the border region of Yucatán, Quintana Roo and Campeche. Its total distribution is considerably larger, as was probably its distribution in Yucatán before massive deforestation. Specimens in the collection of DWR and the University of Kansas Snow Entomological Museum are from Puntarenas, Costa Rica; Oaxaca, Mexico, and Guerrero, Mexico.

Discussion.—Considering its pronounced facial maculation, *M. yucatanica* is similar to the typical form of *M. favosa* but shares no part of its range (Schwarz 1932). The former differs principally in displaying yellow markings at the supralar margins of the mesoscutum and axillae, continuous yellow bands from the first to fifth

Table 1. *Melipona yucatanica*, morphometrics (in mm) of worker holotype, paratypes and allotype male from Mérida, Yucatán, México and male morphometrics of *M. variegatipes* from Montserrat, Lesser Antilles.

variable*.	n	range	mean	s.d.	holotype	allotype	variegatipes
1	10	3.12–3.36	3.27	0.090	3.36	3.08	2.82
2	10	2.00–2.16	2.09	0.046	2.12	1.92	1.80
3	10	2.14–2.28	2.2	0.049	2.24	1.80	1.60
4	10	1.68–1.80	1.75	0.043	1.78	1.36	1.32
5	10	1.88–2.04	1.97	0.047	2.04	1.90	1.64
6	10	0.82–0.88	0.85	0.023	0.88	0.92	0.78
7	10	1.28–1.40	1.33	0.049	1.40	1.12	1.12
8	10	0.88–0.98	0.93	0.034	0.98	0.96	0.90
9	10	1.24–1.50	1.44	0.076	1.48	1.32	1.20
10	10	0.30–0.36	0.32	0.020	0.30	0.24	0.26
11	10	0.48–0.52	0.5	0.015	0.50	0.34	0.36
12	10	0.34–0.40	0.38	0.022	0.34	0.44	—
13	10	0.50–0.56	0.53	0.021	0.52	0.46	0.46
14	10	0.64–0.68	0.65	0.016	0.66	0.60	0.52
15	10	1.02–1.10	1.07	0.030	1.10	0.88	0.80
16	10	0.24–0.26	0.24	0.007	0.26	0.24	0.26
17	10	0.10–0.12	0.11	0.009	0.10	0.06	0.10
18	10	2.24–2.48	2.36	0.069	2.42	3.20	3.04
19	10	1.12–1.20	1.15	0.025	1.16	0.84	0.78
20	10	1.28–1.38	1.34	0.030	1.36	1.04	0.92
21	10	5.76–6.28	6.02	0.159	6.04	6.32	6.24
22	10	2.04–2.32	2.21	0.086	2.22	2.28	2.20
23	10	2.24–2.56	2.44	0.107	2.56	2.04	2.04
24	10	0.96–1.06	1.00	0.036	1.02	0.60	0.60
25	10	1.16–1.32	1.25	0.049	1.32	1.20	1.24
26	10	0.64–0.72	0.69	0.025	0.68	0.48	0.48
27	10	2.14–2.42	2.31	0.096	2.36	2.44	2.20
28	10	2.36–2.64	2.49	0.105	2.64	2.52	2.28
29	10	0.64–0.72	0.68	0.031	0.72	0.68	0.76
30	10	1.40–1.60	1.52	0.072	1.56	1.60	1.52
31	10	9–11	10	—	10	10	10

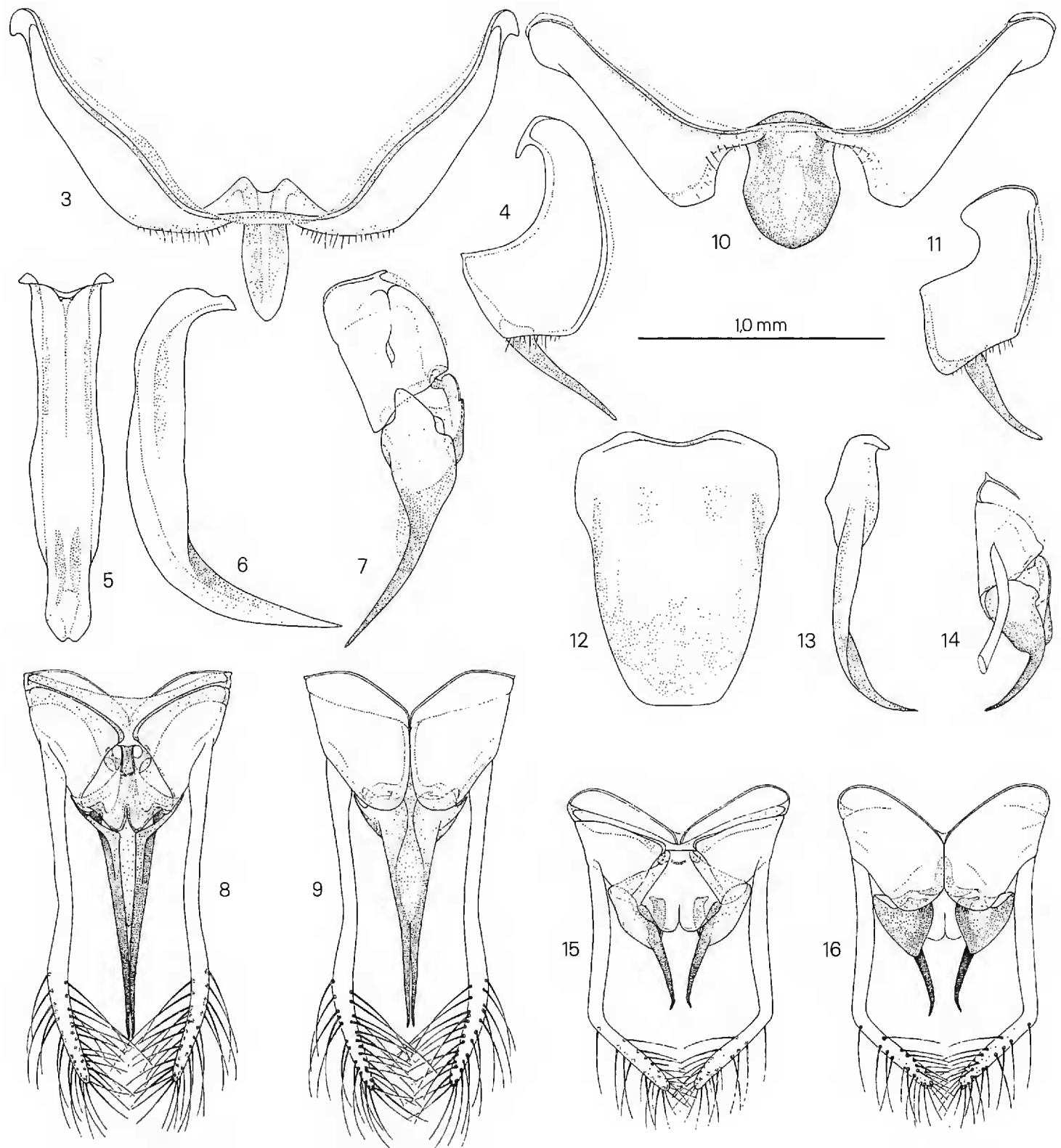
*variables: 1) maximum head width; 2) superior inter-orbital distance; 3) maximum interorbital distance; 4) inferior interorbital distance; 5) compound eye length; 6) compound eye width; 7) distance from clypeus to median ocellus; 8) clypeus length; 9) clypeus width; 10) interalveolar distance; 11) alveorbital distance; 12) ocelloccipital distance (measured from median ocellus in dorsal view); 13) oxellorbital distance (lateral ocellus to orbit); 14) distance between lateral ocelli; 15) distance from alveolus to lateral ocellus; 16) median ocellus diameter; 17) length of malar area; 18) length of flagellum and pedicel; 19) length of scape; 20) length of mandible; 21) fore wing length; 22) fore wing width; 23) metatibia length; 24) maximum metatibial width; 25) metabasitarsal length; 26) metabasitarsal width; 27) length of mesoscutum; 28) width of mesoscutum; 29) length of scutellum; 30) width of scutellum; 31) number of hamuli.

metasomal tergites, gray pilosity on the mesepisternum and the dull micro-punctation of the discal area of the mesoscutum. *Melipona favosa* lacks yellow maculations on the mesoscutum and axillae, as do other forms of this group; the yellow band across the first metasomal tergite is largely interrupted medially; the mesepisternum and mesoscutum are covered with fulvous hairs, and the discal area of the mesoscutum is faintly lustrous. Structure of the male metasomal sternites and

genitalia are very distinct (Figs. 3–16). The male of *M. yucatanica* is unique among the known *Melipona* in possessing the elongate, narrow eighth metasomal sternite (Figs. 5, 6). The corresponding sternite of *M. favosa* is about $2.2 \times$ as long as wide, while that of *M. yucatanica* is over $4.3 \times$ its width. This marked difference may represent a very long separation from the *favosa* group and even a separate origin. Following the key in Schwarz (1932), *M. yucatanica* could be confused with *M. variegatipes* due to the shared characteristic of extensively yellow-ferruginous hind legs, but this bee has no yellow maculations on any part of the body.

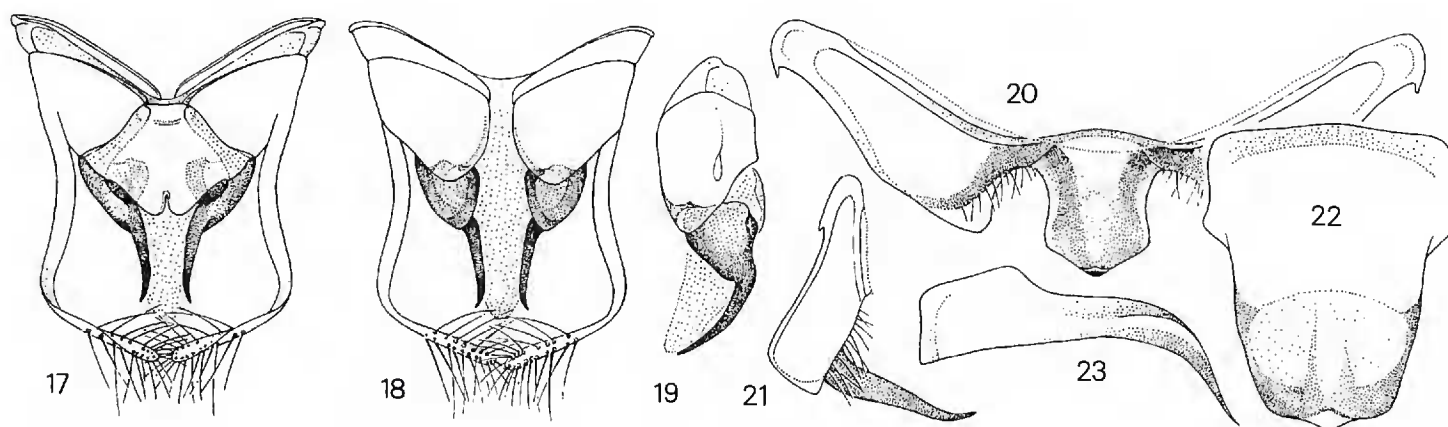
It is now clear that *M. beecheii beecheii* and *M. b. fulvipes* are distinct from *M. yucatanica* and their continental ranges appear to overlap with it completely. Both forms of *M. beecheii* are larger than *M. yucatanica*, and both possess whitish-gray plumose hairs on the clypeus, lacking in *M. yucatanica*. The type specimen of *M. b. fulvipes*, described from Cuba, is supposedly in the Paris Museum. We have only examined two worker bees of the collection of the Portici Museum, Italy. They are labelled Santiago, Las Veras, Cuba, April 10, '26 (interpreted by Schwarz [1932] as 1926). We also examined specimens determined by Schwarz from Cabanas, Cuba; all are very similar to *M. b. fulvipes* from Yucatán and Quintana Roo, Mexico, and also Belize. Typical *M. b. beecheii* is larger than *M. b. fulvipes* (Schwarz 1932), corresponding to bees we have examined from Costa Rica, Nicaragua, Honduras, and Nayarit and Jalisco States in Mexico. Wille (1976: 135) provides a detailed morphometric comparison of Costa Rican *M. b. beecheii* with what he thought to be *M. fulvipes*; its size corresponded closely to those of *M. yucatanica* and it is thus very likely the same bee that we describe. Although Wille states that its distribution ranges from Mexico to Costa Rica and also includes the islands of Cuba and Jamaica, neither he nor we have evidence of its presence on these islands. Wille (1976) reports collecting workers along the Panamerican Highway between Rio Térraba and Palmar Norte. Palmar Norte is approximately 100 km from the Pacific border with Panama.

Comparative distributional data of meliponines and evidence provided by amber meliponine fossils suggest Meliponinae occupied the Caribbean islands and Mexico well before the land bridge of Panama was completed at 3 mybp (Simpson and Neff 1985). Many modern groups of meliponines are certain to have moved across the Isthmus of Panama; some may have crossed during the initial formation for the isthmus in the upper Pliocene (Raven and Axelrod 1975), and there is a suggestion, with little evidence, that some dispersal of continental fauna may have occurred across the Panama gap during the Oligocene-Miocene, 22 to 27 mybp (Halffter 1978). On the other hand, there is substantial geological and biological evidence that an archipelago dispersal route was available in the early Eocene between northwestern South America and Yucatán; sometime in the upper Eocene this connection was broken by the movement of Cuba away from the mainland (Rosen 1985). Fossil evidence definitively attests to the presence of meliponines north of Central America before the Miocene. The modern supraspecific group *Nogueirapis* was described from middle Miocene amber of Chiapas, southern Mexico (Wille 1959, 1962, 1964). The *Nogueirapis* group now occurs from Brazil to Costa Rica. *Proplebeia dominicana* (Wille and Chandler) is known from the Greater Antilles in amber of the Oligocene-Miocene (Michener 1982). This extinct genus has not been found elsewhere and was first described as a modern *Hypotrigona-Liotrigona* or a *Plebeia* (Wille and Chandler 1964; Moure and Camargo 1982a). The related *Plebeia* group exists from southern Brazil to north central Mexico.



Figures 3–9. *Melipona yucatanica*, allotype male from Mérida, Yucatán, México. (3, 4): 7th metasomal sternite, ventral view and profile; (5, 6): 8th metasomal sternite, ventral view and profile; (7–9): genital capsule, profile, dorsal and ventral views. Figures 10–16. *Melipona f. favosa*, male collected in Santa Marta, Magdalena Department, Colombia by G. E. Bohart. (10, 11): 8th metasomal sternite, ventral view and profile; (12, 13) 9th metasomal sternite, ventral view and profile; (14–16): genital capsule, profile, dorsal and ventral views.

The above information could signify that certain meliponine groups were common to Africa, Central and South America in Cretaceous times. Little or no dispersal by island-hopping across the Caribbean is necessary to explain this, and it is one of a number of predictions from cladistic analysis of Caribbean geohistory (Rosen 1985). However, almost no supraspecific groups of meliponines below tribal level occur both in Africa and the neotropics. Despite some close resemblances between



Figures 17–23. *Melipona variegatipes*, male from “Mntserrat, 3.3 WI, H. G. Hubbard Collector.” (17–19): genital capsule, profile, dorsal and ventral views; (20–21): 7th metasomal sternite, ventral view and profile; (22, 23): 8th metasomal sternite, ventral view and profile.

African *Hypotrigena* and the neotropical *Trigonisca* group, and certain groups related to *Plebeia* in southern Brazil and in Africa, meliponine evolution of higher taxonomic groups proceeded independently on the two continents after the upper Cretaceous. Eocene or Miocene exchanges across an archipelago between North and South America seem to better explain the dispersion patterns of *Melipona*. Exchanges by this route are reasonably well established for other organisms, including narrowly specialized solitary bee species and their host plants (Moure and Camargo 1982b; Michener 1982; Simpson and Neff 1985; Graham 1985; Gentry 1985). Furthermore, speciation by another bee group, *Bombus* seems to have been too extensive in South America to result from dispersal across the Panama land bridge. The isthmus was a filter that excluded the passage of species native to xeric or highland habitats, which should have included *Bombus* (Simpson and Neff 1985). The presence of meliponine fossils from the Greater Antilles and the insular existence of *M. variegatipes* in the Lesser Antilles imply an ancient connection between North and South America. The relationship to South America is demonstrated by similarities in *M. variegatipes* and *M. favosa* genitalic structure and worker morphology (Figs. 10–23, Table 1 and Moure 1960, 1971).

The second part of our general argument is that vicariance, the splitting up of previously contiguous populations, led to mutually exclusive distributions of sister species of *Melipona* in Panama and Costa Rica. There are no major vegetational or climatic differences setting these regions apart. All of the *Melipona* of the isthmian area live in lowland forest and build their nests in cavities in living trees (Roubik 1983 and in press). Their foraging habits are broadly similar, but detailed information exists only on the pollen utilization by three species (Roubik and Moreno, unpublished data). We propose that *Melipona* were separated from parent populations during the Eocene or Miocene, diverged ecologically and also specifically in Central America and South America, yet now retain sufficient similarity to competitively exclude their sister species in the isthmian region. The sister species were geographically separated until the late Pliocene. Considering *Melipona* of the region, eight species in all, only one extends from Mexico to South America, *M. fasciata*. Two more range from Costa Rica to Brazil (*M. fuliginosa* and

M. marginata). One bee, *M. crinita*, is restricted to eastern Panama and western South America. The other four species form two closely-related pairs, *M. compressipes*—*M. beecheii* and *M. favosa*—*M. yucatanica*. The first two species have similar male genitalia and their workers are strongly similar in appearance (Schwarz 1932). The ranges of each pair are mutually exclusive in Panama and Costa Rica. Furthermore, a clearly distinct form of *M. compressipes* is found on the large Pacific Panamanian island of Coiba, and *M. favosa* exists on numerous small islands in the Bay of Panama (Roubik in press). These two taxa have several races in South America (Schwarz 1932). Both are certainly adapted to living on islands, some very small, isolated from mainland Panama since the upper Pleistocene.

Only 3 of the more than 40 *Melipona* species are not South American, and it seems likely that a northward dispersal of bees took place across the Caribbean arc. However, the state of our knowledge does not allow recognition of the relatively more primitive or derived taxa, thus does not exclude the possibility of southward dispersal.

Other meliponines indicate wide distribution of bee fauna before formation of the isthmus. Similar vicariant speciation has likely occurred in Central and South American populations. Many supraspecific groups of the Trigonini and certain individual species are distributed throughout the neotropics and probably also inhabited the proto-Antillean archipelago. These include *Lestrimelitta*, *Partamona*, *Nannotrigona*, *Scaptotrigona*, *Plebeia*, *Paratrigona*, *Trigonisca*, *Dolichotrigona*, *Tetragonisca*, *Frieseomelitta*, *Trigona* and *Cephalotrigona*. Since their distributions range from southern Brazil to Mexico and at least *Cephalotrigona capitata*, *Tetragonisca angustula* (= *T. jaty*) and *Lestrimelitta limao* are found throughout this range, it seems that relatively few neotropical meliponine species spread widely after the Panama gap was bridged. The timing of their dispersal may have allowed speciation but not the initiation of insular supraspecific groups. Alternatively, many of the supraspecific groups might have crossed the isthmus only after the formation of the Panama land bridge. As mentioned earlier for *Bombus*, a few dozen of which are restricted to South America, such a high degree of speciation seems unlikely to have occurred since the Pleistocene. So far as we know, at least one or two insular Trigonini in each of the abovementioned supraspecific groups are found north of Panama, making their rate of speciation similar to that of *Melipona*. Therefore, higher Trigonini may have existed in South America and along the proto-Antillean archipelago during the Eocene. Fossil amber *Nogueirapis* of southern Mexico (a bee that generally builds nests in the ground and cannot disperse by rafting or transport in logs) and its current absence north of Costa Rica suggest some regional extinctions of higher meliponine groups. In addition, another South American group having several species there but only one north of Panama, *Ptilotrigona*, is found in southeastern Costa Rica but is absent in the rest of Central America and Panama. These continental taxa trace the demise of previously wide-ranging groups. The distinct distributions of four isthmian *Melipona* provide further evidence of dispersal between North and South America, and subsequent vicariance, preceding formation of the Panamanian land connection.

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